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Published in:
American Naturalist

DOI:
10.1086/682667

Causes and Consequences of Partial Migration in a Passerine Bird

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Submitted July 24, 2014; Accepted May 12, 2015; Electronically published August 11, 2015

Online enhancement: appendix. *Dryad data:* http://dx.doi.org/10.5061/dryad.b5k00.

abstract: Many animal species have populations in which some individuals migrate and others remain on the breeding grounds. This phenomenon is called partial migration. Despite substantial theoretical work, empirical data on causes and consequences of partial migration remain scarce, mainly because of difficulties associated with tracking individuals over large spatial scales. We used stable hydrogen isotopes in claw material to determine whether skylarks *Alauda arvensis* from a single breeding population in the Netherlands had migrated or remained resident in the previous winter and investigated whether there were causes or consequences of either strategy. Age and sex had no influence on the propensity to migrate, but larger individuals were more likely to be residents. The wintering strategy was not fixed within individuals. Up to 45% of individuals measured in multiple years switched strategies. Reproductive parameters were not related to the wintering strategy, but individuals that wintered locally experienced lower future return rates, and this was directly correlated with two independent measures of immune function. Our results suggest that partial migration in skylarks is based neither on genetic dimorphism nor on an age- and sex-dependent condition. Instead, the wintering strategy is related to structural size and immune function. These new insights on causes and consequences of partial migration advance our understanding of the ecology, evolution, and coexistence of different life-history strategies.

Keywords: avian migration, ecological immunology, breeding success, avian life history, carry-over effect.

Introduction

Partial migration occurs when some individuals of a breeding population migrate seasonally to nonbreeding areas while other individuals of the same population remain resident year-round (Gauthreaux 1982; Terrill and Able 1988; Alerstam 1990). Partial migration has been hypothesized to be an evolutionary precursor to full migration (Berthold 1996). It exists in a wide array of taxa including fish, mammals, insects, and birds (Chapman et al. 2011*a*). Studying species that exhibit partial migration offers the unique opportunity to investigate the causes and consequences of migration by comparing migrants and residents within the same population (Adriaensen and Dhondt 1990; Chapman et al. 2011*a*, 2011*b*; Palacin et al. 2011). To date, however, most studies investigating causes and consequences of avian migration have focused on species exhibiting obligate long-distance migration (Alerstam 1990; Berthold et al. 2003; Newton 2008). In contrast, partial migration remains relatively unstudied, despite its potential to provide insight into evolutionary origins and mechanisms of coexistence of different life-history strategies (Cohen 1967; Lundberg 1988; Chapman et al. 2011*a*).

A combination of environmental and genetic factors is hypothesized to underlie partial migration (Schwabl and Silverin 1990; Newton 2008; Chapman et al. 2011*a*; Pulido 2011). The body size hypothesis predicts that individual differences in thermoregulatory efficiency, based on surface/volume ratio, enable larger birds to withstand colder temperatures and longer periods of fasting during harsh winter conditions. Hence, smaller birds improve their probability of survival by migrating to milder areas (Ketterson and Nolan 1976). The dominance hypothesis predicts that socially dominant individuals monopolize food resources in winter and subordinate individuals migrate to avoid competition (Gauthreaux 1982; Smith and Nilsson 1987). Dominance and size are often linked (via age and sex), and, consequently, partial migration often separates age and/or sex classes in winter (Ketterson and Nolan 1976; Ketterson 1979; Able and Belthoff 1998). Alternatively, but not mutually exclusively, the arrival time hypothesis predicts that intrasex competition for breeding territories selects for resi-

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Am. Nat. 2015. Vol. 186, pp. 531–546.
DOI: 10.1086/682667

dency in the territorial sex (Ketterson and Nolan 1976). In all three hypotheses, migration is considered the less optimal strategy ("best of a bad job"). However, partial migration can also evolve when survival in migrants is high and winter survival in residents is density dependent (Taylor and Norris 2007).

The decision to migrate to a geographically disjunct nonbreeding (hereafter wintering) area or to remain resident on a breeding site year-round is likely to affect individual fitness. However, few studies have quantified the consequences of partial migration (Chapman et al. 2011*a*). Previous research demonstrated that resident individuals have a more prolonged molt and lower basal metabolic rates (blue tit *Cyanistes caeruleus* [Nilsson et al. 2011]), higher reproductive success (robin *Erithacus rubecula* [Harper 1985; Adriaensen and Dhondt 1990], American dipper *Cinculus mexicanus* [Gillis et al. 2008]), and lower survival (American dipper [Gillis et al. 2008]). These studies, however, focus on partial migrants with local rather than large-scale migrations, compare migrants and residents that winter together and breed in different areas, or study birds with unknown breeding sites. No study has yet investigated the consequences of partial migration within a breeding population by comparing year-round residents with migrants that fly several hundreds or thousands of kilometers to distinct wintering grounds. Such a study system is essential to quantify the causes and consequences of partial migration and to quantify trade-offs, either within a season or as a carry-over effect to a subsequent season (Newton 2008).

Carry-over effects are becoming well established for obligate long-distance migratory birds. Variation in individual condition and date of departure from nonbreeding areas are known causes of carry-over effects onto the breeding grounds (Marra et al. 1998; Marra and Holmes 2001; Studds and Marra 2005). However, whether there is an underlying physiological mechanism remains unclear (Harrison et al. 2011), although a few studies suggest that hormones are involved (Tonra et al. 2011*a*, 2011*b*; Crossin et al. 2012). Another possible physiological component associated with carry-over effects involves immune function. The immune system promotes survival by reducing the probability of disease-related mortality (Roitt et al. 1998), and migratory birds may need a more diverse immune system as they potentially encounter more pathogens (Møller and Erritzoe 1998; Buehler et al. 2010). Particularly, constitutive innate immunity, which provides the first line of protection, is thought to be of high importance for migratory birds (Buehler et al. 2010). However, immune defenses are costly (Schmid-Hempel 2003; Klasing 2004) and are therefore traded off against competing physiological and behavioral processes (Lochmiller and Deerenberg 2000; Norris and Evans 2000). For example, migratory birds can delay migration when their immune system is challenged (van Gils et al. 2007) or can modulate immune function during migration (Owen and Moore 2008; Hegemann et al. 2012*a*). Yet, delaying migration may affect subsequent reproductive output (Hasselquist 1998), and modulation of immune function might affect survival (Møller and Saino 2004).

To examine the trade-offs within a partial migration system, it is essential to determine the wintering strategy (i.e., migrant vs. nonmigrant) of individual birds. Stable isotope analyses of tissues provide a powerful technique for assigning individuals to particular geographic regions. This method is based on the idea that tissue samples collected at a single capture site estimate the site where that tissue (e.g., feather, claws) was grown (Hobson 1999; Hobson and Wassenaar 2008). Stable hydrogen isotopes, such as deuterium, are particularly useful to determine previous seasonal origin of migratory birds since the deuterium signature shows predictable large-scale patterns that largely vary with latitude (Bowen et al. 2005). This method has successfully assigned migratory birds to wintering or breeding grounds in North America (e.g., Mazerolle and Hobson 2007) and Europe (e.g., Hobson et al. 2004; Bearhop et al. 2005).

In this study, we investigated the causes and consequences (carry-over effects) of year-round residency versus migration in individual skylarks (*Alauda arvensis*). Our study population in the northern Netherlands consists of both residents that winter close to their breeding territory and migrants that winter in SW Europe (Hegemann et al. 2010). As we also know much about their physiology and other fitness-related parameters (Tieleman et al. 2003, 2004; Hegemann et al. 2012*a*, 2012*b*, 2013*a*, 2013*b*), this study population is ideally suited to study the costs and benefits associated with different wintering strategies. We measured the stable isotope deuterium in claws, from four breeding seasons, to establish whether individual birds had migrated or remained resident the previous winter. Repeated sampling of birds across years also revealed whether a strategy was fixed or flexible. To test for carry-over effects related to the winter strategy, we examined reproductive performance (number of nestlings, fledglings, and recruits), physiology (three immune parameters and body condition), morphology (tarsus length and body mass), and return rate. To test for potential causes of choosing a particular wintering strategy, we used repeated within-individual data (hereafter longitudinal data) and compared individuals before and after they migrated or wintered locally, respectively. We predicted that larger individuals have a higher propensity to winter locally. We also predicted innate immunity to be higher in migrants, as they encounter more pathogens. Finally, we did not expect differences in reproductive output that were driven by earlier arrival of residents, because migrants and residents both arrive in their territories 1–2 months before the onset of reproduction (Hegemann et al. 2010).

Methods

Study Species and Methods

Skylarks are widespread temperate zone passerines that breed on the ground in open habitats ranging from natural steppes to modern agricultural farmland across Eurasia (Donald 2004). Birds from northern populations migrate, whereas southern populations are resident year-round and Western European birds are partial migrants (Glutz von Blotzheim and Bauer 1985; Donald 2004; Hegemann et al. 2010).

Skylarks undergo a complete postnuptial molt in adults and a complete postjuvenile molt in birds of the year on the breeding grounds (Glutz von Blotzheim and Bauer 1985). Therefore, instead of feathers we collected claws to obtain a tissue that incorporates deuterium during wintering periods. Bird claws grow continuously, and stable hydrogen isotope analyses from the distal part can provide information about the region the bird visited over a period of several months (Bearhop et al. 2003; Mazerolle and Hobson 2005; Hahn et al. 2014). The length of time that can be traced back prior to sampling depends primarily on the length of the claw (Hahn et al. 2014). Skylarks have a very long back claw that can reach a length of more than 20 mm (Glutz von Blotzheim and Bauer 1985; A. Hegemann, unpublished data). As a result, skylark claws collected during the breeding season have the potential to reveal the wintering strategy during the previous winter.

We caught adult skylarks from our study population at the Aekingerzand in the northern Netherlands (52°55′N, 6°18′E) during the breeding seasons 2006–2009 (Hegemann et al. 2012*b*). Birds were caught at nests while feeding nestlings during May 10–July 20, 2006 ($n = 30$); April 21–July 17, 2007 ($n = 67$); May 4–July 18, 2008 ($n = 49$); and May 4–July 24, 2009 ($n = 40$). Individuals were sampled in 1 year ($n = 88$) and in some cases over multiple years ($n = 27$ in 2 years, $n = 12$ in 3 years, and $n = 2$ in all four study years). We collected blood samples (~150 μL) into heparinized capillary tubes from the brachial vein shortly after capture (median: 5 min; range: 2.25–30 min) to minimize impacts of handling stress on immune parameters (Buehler et al. 2008). Tarsus length, body mass, and wing length were taken after blood collection. Measurements were taken either by A. Hegemann or by our long-term field assistant (R. Voesten). Both trained beforehand to get high consistency among measurements and between ringers. We collected a claw sample by cutting the back toenail with a pair of scissors about 10 mm distal from the skin. Birds were sexed biometrically (Hegemann et al. 2012). Afterward, a metal ring, along with a unique combination of colored rings, was attached to skylark legs if previously unringed, and birds were released. We sampled 60 males (47 once, 11 in two different years, 1 in three different years, and 1 in all four study years) and 69 females (41 once, 16 in two different years, 11 in three different years, and 1 in all four study years).

Claw samples were stored at room temperature until laboratory analyses. Blood samples were stored on ice until returning to the lab later the same day and then centrifuged at 7,000 rpm for 10 min. Plasma and red blood cells were separated and stored at −20°C. Blood sampling was performed under licenses D4743A and DEC5219B of the Institutional Animal Care and Use Committee of the University of Groningen.

Stable Isotope Analyses

Claws were washed in a 2:1 chloroform:methanol solution and air-dried (fume hood) for 48 hours. Claws were transported to the Smithsonian Institution Museum Support Center in Suitland, Maryland, and equilibrated with the local atmosphere for 72 hours. Claw samples varied in length (average: 5.77 mm; range: 1.6–14.3 mm). Long samples were cut into two or more pieces. For short samples, we analyzed the complete sample (average length: 3.02 mm; range: 1.6–4.1 mm; $n = 45$). For long samples, we separately analyzed the basal part and the tip (base: 1.57 mm, 0.7–2.9 mm, $n = 144$; tip: 2.89 mm, 1.45–4.6 mm, $n = 144$). For 9 individuals with long claws, we also sampled one or more middle sections ($n = 16$). Thus, in total we analyzed 349 claw pieces from 186 claw samples collected from 129 individual skylarks over a 4-year period. Samples were loaded into a silver capsule that was crushed, pyrolized at 1,350°C in an elemental analyzer (Thermo TC/EA), and introduced to an isotope ratio mass spectrometer (Thermo Delta V Advantage) via a Conflo IV interface. Four standards were run for every 10 unknowns. Isotope ratios are reported in delta notation relative to Vienna Standard Mean Ocean Water (dD). Analytical error (± 1 SD) was better than 2‰ based on replicate analyses of the same claw ($n = 18$) and replicate analyses of standards. We ran hydrogen (H) standards provided by the International Atomic Energy Agency (IAEA-CH-7) to monitor machine stability and three keratin standards to correct for the combined exchangeable + nonexchangeable H values. The dD values reported include only nonexchangeable H, as determined by a correction using three isotopically different keratin standards (Wassenaar and Hobson 2003).

Assignment of Migratory Strategy

In Europe, stable isotope ratios of H vary with latitude and also over the annual cycle (Bowen et al. 2005). Based on models by Bowen et al. (2005), birds that are resident year-round in northwestern Europe experience stable isotope values from December to February that are depleted

by approximately 20 ppm compared to the breeding season. In contrast, birds from the same population that migrate to winter in southwestern Europe will incorporate deuterium values that are more enriched, by approximately 5–15 ppm, than values during breeding (Bowen et al. 2005; Bowen 2012). Consequently, individual birds from the same breeding population will have different stable hydrogen isotopes depending on their wintering strategy: migrants have enriched deuterium values and residents more negative deuterium signatures compared with values from the breeding period.

Before assigning a wintering strategy to individual claw samples, we first separated claw pieces by year to account for variation between years in deuterium samples (Farmer et al. 2008; Hache et al. 2012). Because of some overlap in deuterium isoclines, we used a conservative assignment rule for each year by assigning only 20% of the most depleted parts to resident birds and the 20% with the most enriched claw pieces to migrants. Claw pieces with intermediate deuterium values were assigned as unknown. By applying this rule, we were able to assign birds as resident and migrants, respectively, with the following isotopic values: 2006, resident: −67.4‰ to −64.3‰, migrant: −51.0‰ to −48.1‰; 2007, resident: −69.9‰ to −60.2‰, migrant: −47.4‰ to −31.0‰; 2008, resident: −70.1‰ to −60.6‰, migrant: −56.6‰ to −27.0‰; 2009, resident: −83.7‰ to −69.1‰, migrant: −50.8‰ to −34.4‰. The difference between the most enriched resident and the most depleted migrant, that is, the unclassified range, was on average −14.6‰. Our assignment criteria are conservative when compared with published data of variation in deuterium estimates from tissues of known origin (Wunder et al. 2005; Rocque et al. 2006; Langin et al. 2007) and with the previously used difference of 9‰ that was established to reflect differences in dispersal distances (Studds et al. 2008).

Based on the most extreme isotope values of all pieces of each claw, an individual was classified as migrant, resident, or unknown. Using this assignment rule, in 3 of the 187 complete samples the bird was simultaneously classified as resident and migrant based on different pieces of a single claw. In these cases we used the strategy reflected by the basal part of the claw to capture the recent wintering strategy. Across all four study years, we were able to assign 107 individuals to a wintering strategy; 79 individuals remained unclassified (2006: 6 migrants, 6 residents, 18 unknown; 2007: 17, 19, 31; 2008: 16, 17, 16; 2009: 12, 14, 14). For 32 of these individuals we knew the exact age because birds had been ringed as nestlings.

Reducing the number of unclassified individuals would be possible by assigning 25% (rather than 20%) of the most depleted parts to resident birds and the 25% (rather than 20%) with the most enriched claw pieces to migrants. Results with respect to the causes and consequences of partial migration (see "Results") were qualitatively similar when applying this rule compared to the 20% assignment rule. However, the smaller difference in the unclassified range seems less robust when viewing published data on variation in deuterium estimates. Hence, we report only results using the 20% assignment rule.

To test our assignment criteria, we conducted two validation tests. First, we analyzed the claw sample of a single individual that was proven by means of radiotelemetry to winter in the study area (Hegemann et al. 2010). Based on our assignment rules, this bird was indeed classified as a resident by the deuterium signature of −62.7‰ in a proximal piece of claw. Second, to validate the deuterium estimates within individual birds, we compared the tips of the right claw and the left back claw for 14 individuals. The average stable deuterium difference between right and left was −0.53‰ ($\pm$1.08 SE; $n = 14$). Knowing that the analytical error was less than 2‰ (see "Stable Isotope Analyses") and that the two pieces of an individual claw varied in length (mean difference: 0.6 mm; range: 0.1–1.9 mm) suggested that this repeatability is high.

Immune Assays

We used two assays that focus on the innate immune system. This subsystem is an important first line of defense (Janeway et al. 2005), is related to antigen exposure (Horrocks et al. 2012, 2015), and shows consistencies over longer timescales (Hegemann et al. 2012*a*). These points coordinate with our main hypotheses regarding different wintering strategies in a partial migrant. (1) We used a hemolysis-hemagglutination assay to quantify titers of complement-like lytic enzymes and nonspecific natural antibodies from preserved plasma samples (Matson et al. 2005; Hegemann et al. 2012). Although high baseline values of lysis titers are thought to be beneficial in terms of general immune defense, lysis titers increase following an immune challenge (Hegemann et al. 2013*b*). Agglutination titers vary between annual-cycle stages and between years in skylarks (Hegemann et al. 2012*a*), but they are more genetically controlled than other immune parameters (Versteegh et al. 2014) and are usually unaffected by acute sickness responses (Matson et al. 2005; Hegemann et al. 2013*b*). Scans of individual samples were randomized among all plates and scored blindly to year and migratory strategy (by A. Hegemann). (2) We used a commercially available colorimetric assay kit to quantify haptoglobin concentrations in plasma samples (Hegemann et al. 2012*a*; Matson et al. 2012). Haptoglobin is an acute-phase protein that is released from the liver during a pathogenic challenge. Skylarks appear to rely on relatively high constitutive concentrations of haptoglobin rather than inducing its production when needed (Matson 2006; Hegemann et al. 2013*b*).

Reproductive Performance and Return Rates

In each of the four study years, the breeding population was intensively monitored. We ringed all nestlings with a metal ring and a unique combination of color rings at about 8 days old—the approximate age that skylark nestlings fledge (Praus et al. 2014). Thus, the number of fledglings is defined as the number of ringed nestlings. Capture and ring readings at or near the nest revealed the identity of the parents. We examined return rates of adults (survival) and young (recruitment) by ring readings and catching parents on nests. As detection probabilities of ringed birds during the breeding season were almost 100% during the study years (A. Hegemann, unpublished data), and as we have no indication that detection rate differed between strategies, we used the percentage of resighted birds per year as the return rate. Because resident skylarks left their territories outside the breeding season and spent the winter on nearby agricultural fields surrounding the study area (Hegemann et al. 2010), we also apply the term "return rates" for residents. Due to high nest predation rates (Praus et al. 2014) and the cryptic behavior of skylarks, we likely missed breeding attempts that were de-predated in an early phase. Hence, instead of calculating potentially unreliable data on the onset of reproduction, we analyzed only data of nests containing nestlings because feeding behavior is more obvious to detect and we are confident in finding close to all successful broods.

Statistical Analysis

Statistical analyses were performed using linear mixed models (function lme, package nlme) and generalized linear mixed models (function lmer, package lme4) with the program R, version 2.15.0 (R Development Core Team 2012). We compared migratory ($n = 51$) to resident ($n = 56$) skylarks for each response variable (table 3) and included as explanatory variables the wintering strategy, year, sex, and Julian day (the latter not in analysis of tarsus length). We also included the two-way interaction of wintering strategy with year and the two-way interaction of wintering strategy and sex. Individual identity was always included as a random effect to avoid pseudoreplication. To analyze the number of nestlings, fledglings, and recruits, a generalized linear mixed model with a Poisson error structure was applied. Return rates (migrants: $n = 44$; residents: $n = 50$) were analyzed with the same model type and a binomial error structure. To test whether migrants and residents differed in the breeding season prior to a winter or whether differences developed over the winter, we used repeated within-individual data (longitudinal data) and compared individuals before and after they migrated ($n = 15$) or wintered locally ($n = 10$), respectively. To accomplish this, we used (generalized) linear mixed models as described above. We included wintering strategy, year, sex, Julian day, and time point (two levels: before or after the winter) in the model as main effects. We also included the three-way interaction of wintering strategy, year, and time point. To test whether future return rates could be predicted by any immune measurement, we sequentially included the interaction between the three immune parameters with strategy in a generalized linear mixed model with binomial error structure with individual identity as random effect and sex and year as covariates. We always started with the full model and then simplified using a backward elimination based on a log likelihood ratio test with $P < 0.05$ as the selection criterion ("drop1" in R) until reaching the minimal adequate model. Model assumptions were always checked on the residuals of the final model. A corrected Akaike information criterion model selection approach led to qualitatively similar results (appendix, "Results of Model Selection Based on an Akaike Information Criterion Approach"; appendix available online); tables and text give statistics and coefficients of the backward selection procedure. The fact that both approaches led to qualitatively similar results stresses the robustness of our conclusions. All data underlying the statistical analyses in this manuscript are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.b5k00 (Hegemann et al. 2015).

Results

Among the 107 claw samples that we assigned to one of the two strategies based on their isotope signatures, we identified 21 male and 30 female migrants and 28 male and 28 female residents. There were no sex or age class differences between strategies among birds that survived any given winter (Fisher exact test, always $P > 0.42$; table 1). For 17 pairs, we were able to assign a wintering strategy to both the male and the female. In four cases, both were migratory; in six cases, the male was a resident and the female a migrant; and in seven cases, the male was a migrant and the female a resident. We found no situations in which both individuals were residents.

Consistency versus Switching of Strategies

For 20 skylarks we assigned a wintering strategy for multiple years ($n = 12$ for two winters; $n = 7$ for three winters;

Table 1: Wintering strategy of skylarks with known age split per sex

Age	Migrant (M/F)	Resident (M/F)
First winter	3/3	3/5
Second winter	4/3	1/4
Third winter	1/3	2/0

Note: All birds have been ringed as nestlings. M = male; F = female.

$n = 1$ for four winters; table 2). Nine individuals used both strategies, and 11 individuals used only one strategy; there was no significant difference in the number of individuals either using only one strategy or switching between strategies ($\chi^2 = 0.1$, $P = 1$). Among the 29 cross-winter comparisons, individuals switched strategies 9 times compared to 20 occasions where the strategy remained the same, a nonsignificant difference in frequencies ($\chi^2 = 1.45$, $P = 0.23$; table 2). Birds switched from either being first migratory to being resident in a later winter ($n = 4$) or vice versa ($n = 5$), and this was not age related (*t*-test, $t = 0.50$, $P = 0.63$).

Postwinter Comparisons

Migrants differed from residents in structural size. Migratory skylarks had a tarsus length that was, after correction for sex and year differences, on average 0.33 mm (1.4%) shorter than that of resident birds, a significant difference (fig. 1*A*), but migrants and residents did not differ in wing length (table 3). Resident skylarks were, after correction for differences between sexes, years, and Julian day, on average 0.81 g (2.2%) heavier than their migratory conspecifics (fig. 1*B*). This effect was independent of sex (interaction strategy × sex: $\chi^2 = 0.57$, $P = 0.45$, $N = 105$) and nonsignificant when taking into account tarsus length as measure of structural size ($\chi^2 = 0.61$, $P = 0.43$, $N = 105$). Tarsus length and body mass were significantly positively correlated ($\chi^2 = 28.37$, $P < 0.001$, $N = 105$; fig. 2).

Migrants and residents differed for some indexes of immune function and the probability of return in a subsequent year. In all years, migrants had, on average, higher, though not statistically significant, lysis titers than resident skylarks (fig. 1*C*; table 3). Residents and migrants did not differ in agglutination titers (table 3; fig. 1*D*). Haptoglobin concentrations in migratory skylarks differed from those in resident individuals in some years (table 3; fig. 1*E*). Skylarks that migrated the previous winter had a significantly higher chance of returning after the following winter (for all 4 years combined: migrants, 77%; residents, 60%; $N = 93$, $P = 0.01$; table 3).

Some indexes of immune function correlated with future return rates. Low haptoglobin concentrations were significantly correlated with a higher probability of future return ($\chi^2 = 4.3$, $P = 0.038$, $N = 88$), independent of winter strategy (interaction haptoglobin × strategy: $\chi^2 = 0.0$, $P = 0.77$). Lysis titers were significantly correlated with future return rates in residents but not in migrants (interaction lysis × strategy: $\chi^2 = 3.67$, $P = 0.05$, $N = 91$); residents that did not return in the future had significantly lower lysis titers compared to returning residents (fig. 3). There was no relation between agglutination titers and the probability of future return (interaction agglutination × strategy: $\chi^2 = 0.33$, $P = 0.56$, $N = 91$; agglutination: $\chi^2 = 0.27$, $P = 0.60$, $N = 93$).

Reproductive parameters (number of nestlings, fledglings, and recruits) did not differ between migrant and resident skylarks (table 3; fig. 1*G*, 1*H*). Pairs consisting of two migrants, a migrant male and a resident female, or a resident male and a migrant female did not differ in the number of fledglings they produced ($\chi^2 = 1.04$, $P = 0.59$, $N = 15$).

Longitudinal Data

For 26 cases (winter 2007–2008: $n = 16$; winter 2008–2009: $n = 10$) individuals had also been sampled during the breeding season prior to the winter (hereafter breeding season X). Skylarks that were resident in winter had higher lysis titers than migrants in breeding season X, but lysis titers of residents had decreased in breeding season X + 1 and remained constant in migratory individuals (interaction strategy × time point: $\chi^2 = 5.2$, $P = 0.02$; fig. 4*A*). Skylarks that were resident in winter increased in size-corrected body mass from one breeding season to the next, while skylarks that migrated had lower size-corrected body mass the following breeding season (interaction strategy × time point: $\chi^2 = 6.49$, $P = 0.01$; fig. 4*D*). Agglutination titers, haptoglobin concentrations, and reproductive parameters did not develop differently between breeding seasons when comparing individuals that migrated with individuals that remained resident (always $\chi^2 < 1.74$, $P > 0.19$; fig. 4; table A11; tables A1–A11 available online).

Tarsus Length versus Consistency and Switching of Strategies

For 20 individuals we have repeated wintering strategies. Although based on a limited sample size, comparing tarsus length among switchers, obligate migrants, and obligate

Table 2: Number of individual skylarks for which we could assign a wintering strategy for multiple years based on the stable hydrogen value in their claws

N years	Always R	Always M	R → M	M → R	R → R → M	R → M → M	M → M → M → R
2	2	4	3	3	NA	NA	NA
3	1	4	0	0	1	1	NA
4	0	0	0	0	0	0	1

Note: The top row gives different possible combinations of strategies in multiple winters. R = resident; m = migrant; NA = not applicable.

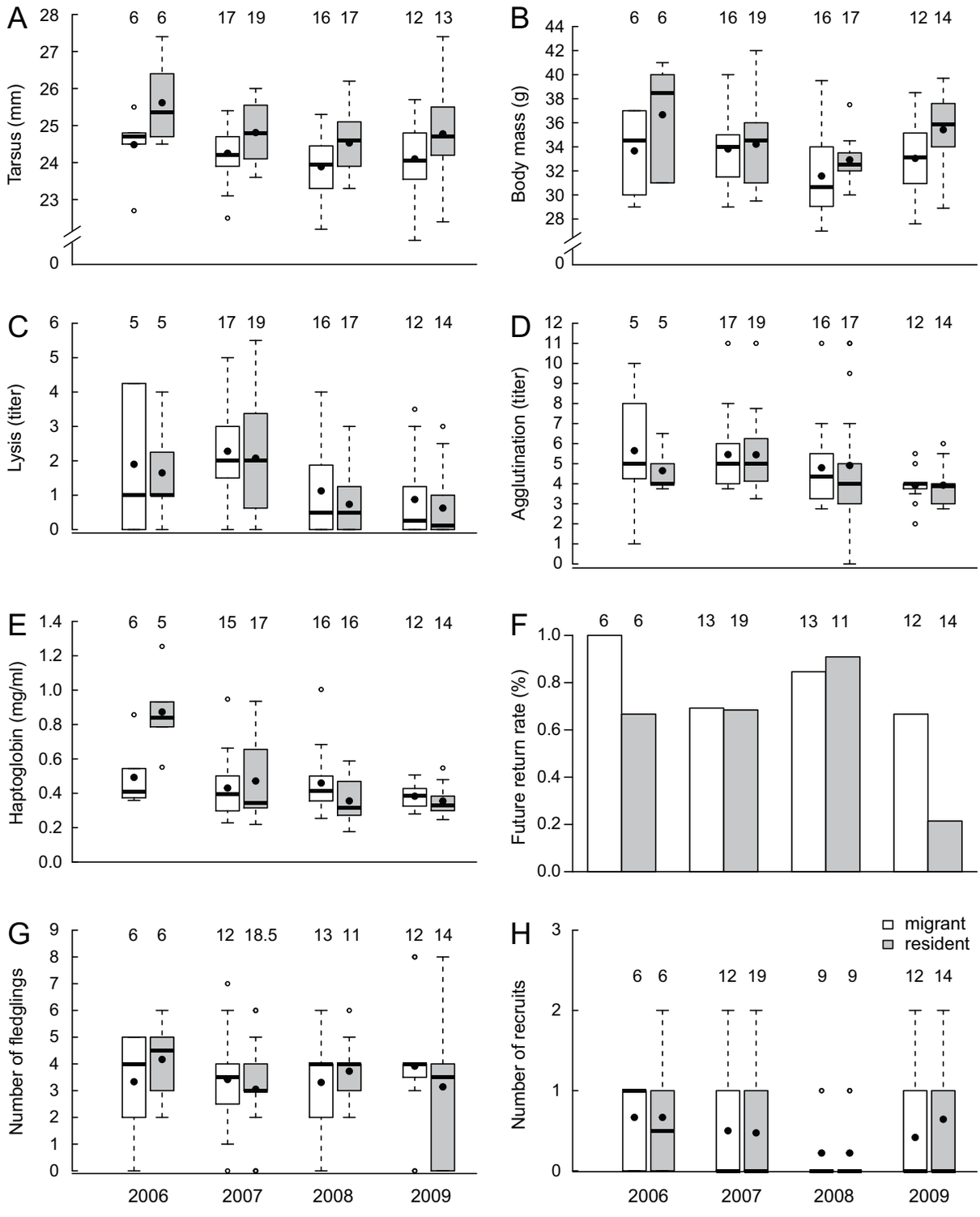

Figure 1: Tarsus length (*A*), body mass (*B*), lysis titers (*C*), agglutination titers (*D*), haptoglobin concentrations (*E*), future return rates to the next breeding season (*F*), number of fledglings (*G*), and number of recruits (*H*) of skylarks in relation to their wintering strategy in the preceding winter. Data are collected during the breeding season. The wintering strategy is determined by means of stable hydrogen analyses of claw samples. Plotted are raw data, not effect sizes. Horizontal lines in the boxes give the median, filled circles show the mean, boxes cover the 25%–75% range, and vertical lines cover the 5%–95% range. Open circles show extreme data points, which were included in the analyses. For future return rates, bars depict means. Numbers represent sample sizes of individual birds for which information of the corresponding response variable was available.

Table 3: Statistics and coefficients of the linear mixed models of measures of immune function, reproductive parameters, body mass, tarsus length, and future return rates of skylarks during the breeding season in relation to their wintering strategy (WS) in the previous winter

	Explanatory variables																	
	WS				Year		Sex				Julian day				WS × year		WS × sex	
Response variable	χ^2/F	β^b	SE	P	χ^2/F	P	χ^2/F	β^a	SE	P	χ^2/F	β	SE	P	χ^2/F	P	χ^2/F	P
Lysis titer	3.01	…	…	.083	28.28	**<.001**	.16	…	…	.688	15.79	.02	.006	**<.001**	1.04	.791	1.44	.230
Agglutination titer	.08	…	…	.771	7.15	.067	.03	…	…	.087	.05	…	…	.830	.44	.932	.05	.821
Haptoglobin (mg/mL)	.11	…	…	.734	9.33	**<.001**	.48	…	…	.483	.18	…	…	.670	16.49	**<.001**	3.61	.058
No. nestlings	.63	…	…	.426	3.03	.388	.29	…	…	.588	5.86	−.004	.002	**.016**	1.13	.769	.00	.953
No. fledglings	.20	…	…	.658	.65	.886	.00	…	…	.948	.39	…	…	.534	2.36	.501	.03	.870
No. recruits	.08	…	…	.370	3.49	.322	.36	…	…	.549	.07	…	…	.797	.26	.966	1.54	.214
Return rate	4.28	−1.11	.55	**.039**	10.82	**.013**	.00	…	…	.994	10.99	.04	.01	**<.001**	5.45	.141	1.63	.202
Body mass (g)	4.92	.81	.37	**.026**	12.74	**.005**	49.17	3.93	.49	**<.001**	16.07	−.03	.008	**<.001**	3.86	.278	.57	.449
Wing length (mm)	.00	…	…	.968	6.87	.076	121.19	9.11	.54	**<.001**	1.04	…	…	.309	3.44	.329	.10	.749
Tarsus length (mm)	10.97	.33	.10	**<.001**	10.39	**.016**	37.65	1.15	.17	**<.001**	…	…	…	…	3.90	.272	2.81	.094

Note: The WS is determined by means of stable hydrogen analyses of claw samples. Individual bird identity was included as a random effect to avoid pseudoreplication. Estimates (β) along with their standard errors (SE) are shown only for significant terms. Final models contain only significant explanatory variables. P values <0.05 are shown in bold.

[a] Reference is male.

[b] Reference is resident.

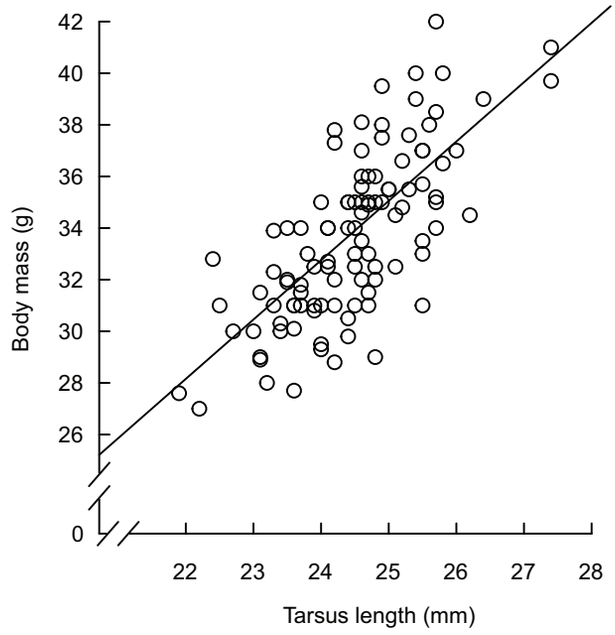

Figure 2: Correlation between body mass and tarsus length in skylarks. Plotted are raw data; the regression line is based on estimates from the model, that is, corrected for effects of sex, year, and Julian day.

residents revealed that the individuals that switched tended to have a tarsus length intermediate to that of obligate residents and obligate migrants (fig. 5).

Discussion

By using stable hydrogen isotopes to distinguish migratory versus resident individuals, we found that partial migration in skylarks was not a fixed strategy within individuals. Over the four years of our study, 45% of individuals sampled across multiple winters switched strategies. The wintering strategy was related to an individual bird's structural size. Birds that had remained resident the previous winter were larger than skylarks that had migrated. Individuals that remained resident in the Netherlands also had a lower probability of future local return, and this was significantly correlated with low lysis titers. Independent of wintering strategy, future return rates were lower in birds with high haptoglobin concentrations. Longitudinal data showed that compared to migrants, residents had higher lysis titers the prior breeding season but lower lysis titers in the breeding season after remaining in the Netherlands for the winter. Interestingly, we found no association between wintering strategy and reproductive success, despite carry-over effects from wintering conditions on reproductive performance being well established for long-distance (e.g., Marra et al. 1998; Marra and Holmes 2001; Studds and Marra 2005) and short-distance (Adriaensen and Dhondt 1990; Dale and Leonard 2011) migratory birds. We also found no indication of assortative mating among birds with the same wintering strategy, while such assortative mating (although two overwintering locations rather than migratory birds vs. resident birds) is documented for blackcaps *Sylvia atricapilla* (Bearhop et al. 2005). Our data suggest that partial migration is a condition-dependent strategy based on the size of individuals and is fine-tuned by difference in immune function. The wintering strategy also has carry-over effects on immune function and future return rate (fig. 6). In the following sections we will discuss each result and outline how it helps to understand the ecology and evolution of partial migration, especially in light of the well-developed theoretical framework and empirical work from fishes and birds. We will also discuss the relevance of our findings for conservation efforts for this rapidly declining species.

Our finding that individuals switch between strategies suggests that partial migration in skylarks is not based on a genetic dimorphism related to the propensity to migrate. Similar wing lengths between migrants and residents further support this idea. Switching strategies between win-

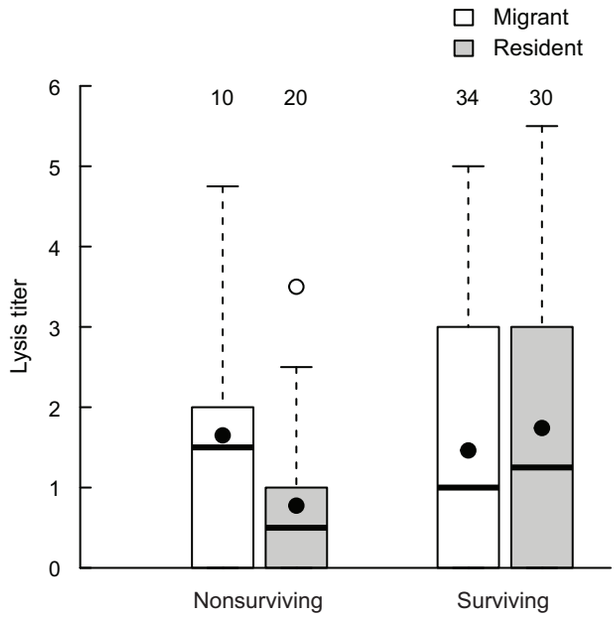

Figure 3: Lysis titers measured during the breeding season (Y) for skylarks that had migrated or remained resident in the previous winter. The categories nonsurviving and surviving separate those birds that did not return to the study area in the next breeding season ($Y + 1$) from those individuals that did return. Horizontal lines in the boxes give the median, filled circles show the mean, boxes cover the 25%–75% range, and vertical lines cover the 5%–95% range. Open circles show extreme data points, which were included in the analyses. Numbers represent sample sizes of individual birds.

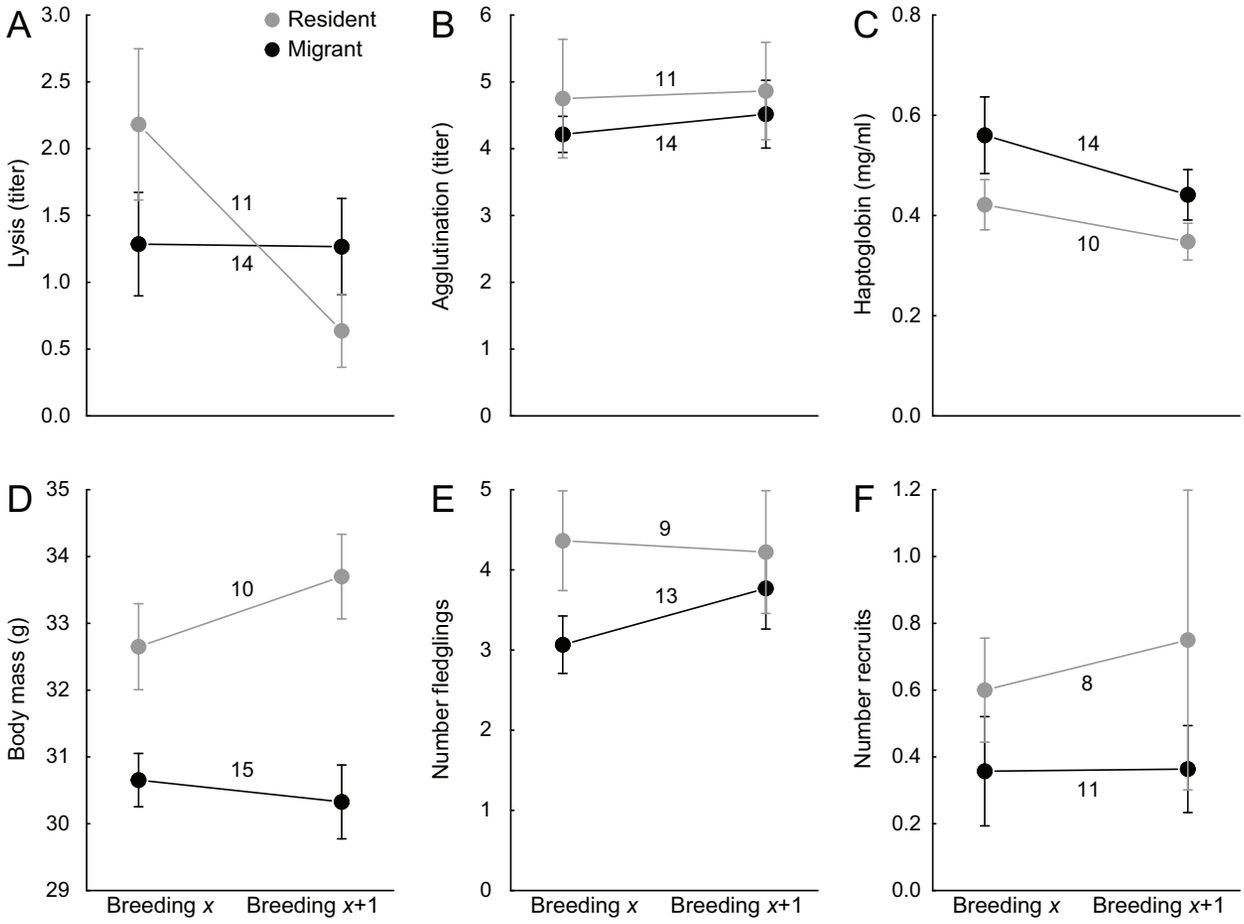

Figure 4: Within-individual changes in lysis titer (*A*), agglutination titer (*B*), haptoglobin concentrations (*C*), body mass (*D*), number of fledglings (*E*), and number of recruits (*F*) between the two breeding seasons, prior to and following the winter for which we identified the wintering strategy. Plotted are raw data, not effect sizes. Bars depict means and standard errors. Numbers represent sample sizes of individual birds for which information of the corresponding response variable was available.

ters has been reported in several other partially migrating songbird species but is usually related to sex and age (Schwabl 1983; Able and Belthoff 1998; Fudickar et al. 2013). That skylarks can switch strategies independent of age and sex supports earlier theoretical models predicting that partial migration is not based exclusively on genetic factors but also driven by environmental conditions (Cohen 1967; Berthold 1991). The fact that similar findings have been reported for fish (Brodersen et al. 2014) suggests that partial migration may be driven by similar mechanisms across taxa.

Smaller-bodied skylarks were more likely to have been migratory the previous winter, while larger skylarks were more likely to have been residents. This pattern is consistent with both the dominance hypothesis and the body size hypothesis (Ketterson and Nolan 1976; Gauthreaux 1982). Larger individuals may have an advantage to successfully overwinter in northern latitudes. Especially under harsh conditions a larger body may provide significant advantages for thermoregulation. Furthermore, larger individuals may possibly also be able to store bigger fat reserves and hence may be able to survive longer periods of fastening. Further support for the dominance hypothesis comes from the fact that winter food for skylarks in the Netherlands appears limited (Geiger et al. 2014). Moreover, resident skylarks are in winter accompanied by skylarks originating from more northern and eastern populations (Hegemann et al. 2010). These birds are longer winged and potentially larger than Dutch skylarks (Glutz von Blotzheim and Bauer 1985; Hegemann et al. 2012). Given the limited food access in winter, only the biggest individuals of the Dutch population may be able to compete for food in winter, while small individuals may be forced to migrate. In contrast, we found no support for

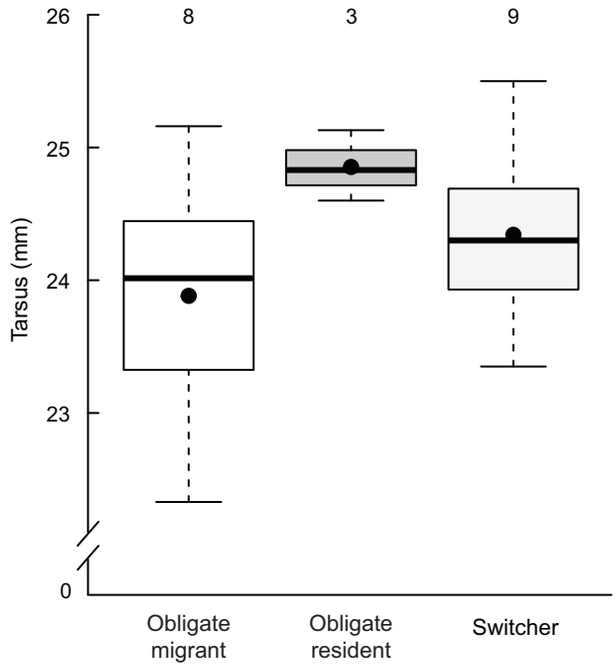

Figure 5: Tarsus length of individual skylarks for which we could assign a wintering strategy for multiple winters. Horizontal lines in the boxes give the median, filled circles show the mean, boxes cover the 25%–75% range, and vertical lines cover the 5%–95% range. Numbers represent sample sizes of individual birds.

the early-arrival hypothesis. This supports the idea that early arrival is not a major evolutionary force for partial migration (Boyle 2008).

There seems to be a paradox between the fact that some individuals switch strategies between years and the overall finding that migrant birds tend to be smaller bodied than residents. Although based on a limited subset of birds, the individuals that switched strategies showed a trend toward having a tarsus length intermediate to that of obligate residents and obligate migrants. Hence, the existence of switching does not necessarily contradict our finding that larger skylarks are more likely to be resident and smaller individuals more likely to be migratory. Intermediate-sized skylarks may have the highest probability to switch strategies, because they can be relatively large compared with other overwintering skylarks in one winter but relatively small compared with conspecifics in another winter (fig. 6). This pattern can arise for two reasons. First, the number of overwintering larger skylarks from more northern populations may vary with their breeding success. Second, cohorts of birds hatched in a given year can differ in structural size from cohorts hatched in other years, depending on environmental conditions during ontogeny (Van Noordwijk et al. 1988). Our study therefore supports the idea that partial migration is a (partially) conditional strategy with a frequency-dependent choice (Lundberg 1988). Such a strategy can maintain partial migration over evolutionary time (Lundberg 1988; Chapman et al. 2012). A conditional strategy has been identified to also drive partial migration in fish (Brodersen et al. 2008, 2014; Chapman et al. 2012) and might hence be a widespread mechanism of partial migration.

Wintering strategy had carry-over effects on indexes of immune function. It has been hypothesized that migrants face higher risks of infection than residents because the former encounter more types of pathogens (Møller and Erritzoe 1998). Our data on lysis titers support this idea. Haptoglobin concentrations were either higher or lower in migrants compared to residents, depending on the year. In skylarks, baseline values as measured in this study potentially reflect the regulation of the immune system in response to risks of inflammation (Hegemann et al. 2012*a*), which may have been particularly high for residents in the winter of 2005–2006. Agglutination titers did not differ between skylarks with different wintering strategies. Since these natural antibody titers are more genetically controlled than other immune parameters (Versteegh et al. 2014) and are usually unaffected by acute sickness responses (Matson et al. 2005; Hegemann et al. 2013*b*), one would expect agglutination titer to differ between residents and migrants only when partial migration is based on a strong genetic dimorphism and when strategy switching does not occur.

The wintering strategy had carry-over effects on the probability of future return, and this was linked to immune function. We have shown previously that the reaction of the immune system to an experimentally increased workload can take weeks to months (Hegemann et al. 2013*a*). In addition, we found that immune patterns during the breeding season can predict mortality in the following winter (Hegemann et al. 2013*a*). Combining those findings with those of this current study of carry-over effects from winter to breeding season, we suggest that inclement winter conditions, whether spent close to the breeding grounds or after southerly migration, may compromise the immune system during the following summer. This in turn leads to increased mortality during the next winter, through reduced resistance against viruses, diseases, and parasites (Hegemann et al. 2013*a*), and may represent a mechanistic link between carry-over effects and survival.

Our longitudinal data show that skylarks that remained resident had higher lysis titers in the previous breeding season compared to birds that migrated later. In residents the titers decreased over winter, while in migrants the titers remained constant on an intermediate level. Very high lysis titers may indicate that birds are undergoing an infection (Hegemann et al. 2013*b*). Current infections can hamper the migratory behavior of wild birds (van Gils et al. 2007). Therefore, we hypothesize that current infec-

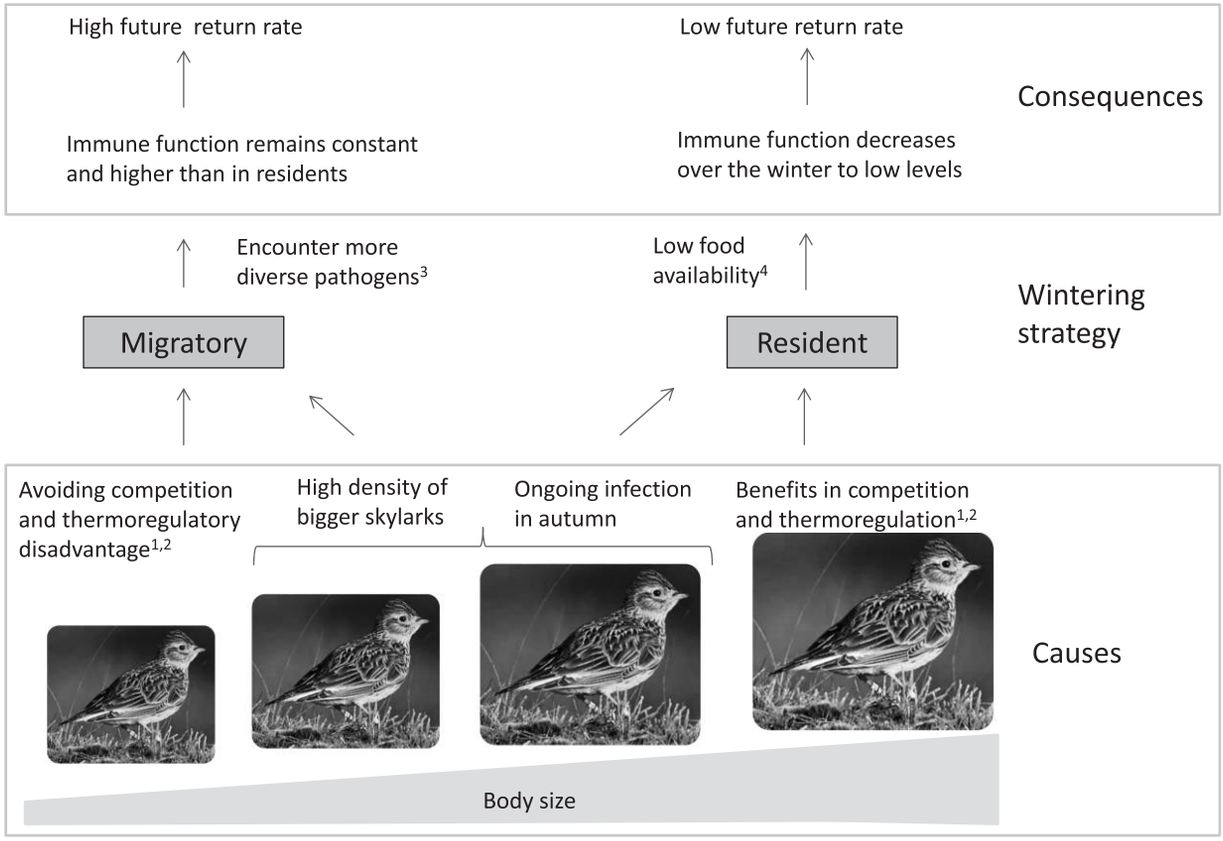

Figure 6: Schematic synthesizing results of the causes and consequences of partial migration in skylarks. Probability of migration increases with increasing body size, with individual differences in thermoregulatory efficiency and dominance abilities as hypothesized causes. Individuals of intermediate size can be either resident or migrant. Infections and density of larger skylarks may influence the decision to migrate or remain resident. Migratory skylarks encounter more and diverse pathogens, resulting in constant and high levels of immune function; this relates to high future return rates. In contrast, resident skylarks experience low food availability, and immune function decreases to low levels; this relates to low future return rates. References: 1 = Ketterson and Nolan (1976); 2 = Gauthreaux (1982), Smith and Nilsson (1987); 3 = Møller and Erritzoe (1998), Buehler et al. (2010); 4 = Geiger et al. (2014).

tions (indicated by very high lysis titers during breeding) may favor skylarks to remain resident in winter. This represents an additional but not mutually exclusive explanation for why individuals switch strategies and why partial migration is not related to age and sex. Thus, it may explain among-individual variation in the propensity to engage in partial migration that cannot be explained by the body size and dominance hypotheses or by a frequency-dependent choice. Taken together, our data suggest that immune function might be involved in whether a bird migrates or remains resident. Hence, our study builds on evolutionary theory of migration (Berthold 1999) and on pervious work suggesting that individual condition influences the wintering strategy of partial migrants in birds and fish (Boyle 2008; Brodersen et al. 2008, 2014). Our results expand on this by finding that immune function, as one of the main physiological regulators of body condition, is related to partial migration. Furthermore, immune function is then also affected by the wintering strategy, which in turn affects future survival probability.

That resident skylarks, when compared with migratory conspecifics, are less likely to return to breed in future years has important implications for conservation planning. The skylark, as well as many other farmland birds, continues to rapidly decline in many (western) European countries and especially in the Netherlands (SOVON 2002; PECBMS 2009). We have shown previously that skylarks wintering in the northern Netherlands experience a lack of energy-rich food, and this may minimize the ability of skylarks to meet daily energy requirements (Geiger et al. 2014). Our study is consistent with and builds on this research by demonstrating that skylarks that winter in the Netherlands also have reduced immune function and lower future return rates. Increasing supply of high-quality food

during winter might help to solve this problem, since maintaining and activating the immune system requires energy and specific nutrients (Klasing 2004; Hegemann et al. 2012*b*, 2013*a*). An additional indication that wintering in the Netherlands is a less successful strategy comes from our finding that only 15% of the skylarks were consistent residents while more than 40% were consistent migrants. Overall, conservation plans should recognize the possible consequences of winter conditions and limited food supply and include measures to increase habitat suitability during winter to help increase adult survival in skylarks.

To summarize, by linking individual wintering strategies to the physiology, morphology, reproduction, and return rates in skylarks, we gained new insights on causes and consequences of partial migration among individuals from the same breeding population (fig. 6). Applying this integrative approach allowed us to provide novel insights into the evolution of partial migration. We show that the individual decision (defined here as an adaptive choice rather than a cognitive performance) to migrate or remain resident is a condition-dependent choice based on the size of individuals. Similar findings in partial migration of fish suggest that individual size and body condition are traits involved in the evolution of partial migration across taxonomic borders. In skylarks, this decision might be fine-tuned by their physiological status and can potentially explain the occurrence of switching. Overall, we provide first empirical evidence for theoretical models that avian partial migration is a continuum between the extremes of genetically controlled obligate partial and facultative partial migration based on age- and sex-related individual condition (Lundberg 1988; Newton 2008). That the immune system might be involved in determining individual decisions to migrate or remain resident opens a new field of understanding as to the causes and consequences of partial migration. Links to the physiology underlying individual body condition and the controls of partial migration had been missing so far. As individuals are the currency of natural selection, this improved understanding of what factors determine whether individual animals become either resident or migratory will help us unravel the ultimate factors underlying the evolution of partial migration, understand population-level dynamics, and predict future microevolutionary processes in migratory species. While we found clear costs of residency in terms of reduced future return rates, we could not detect any benefits of residency. In our view, there are two potential explanations. First, to balance the cost relative to reduced future survival, there could be benefits in reproduction that we have not detected because they become evident only in certain years, when reproductive success may be significantly higher than in migrants. Alternatively, there really are no benefits of residency (anymore), and the costs in survival are simply contributing to the ongoing sharp decline of this species. Rapid advances in our ability to track small animals over time and space will provide exciting opportunities for further advancing our understanding of partial migration and also other evolutionary and ecological questions with respect to trade-offs of different behavioral strategies in migratory and nonmigratory species.

Acknowledgments

We thank M. Grysan, G. Mays, and R. Voesten for help with fieldwork and K. D. Matson for discussions. Comments by T. Alerstam, K. D. Matson, J.-Å. Nilsson, N. Sapir, and two anonymous reviewers helped to improve the manuscript. Stable isotope analyses were conducted at the Smithsonian Institution Stable Isotope Laboratory by N. Diggs and C. France. Funding came from BirdLife Netherlands, a Rosalind Franklin Fellowship, the Netherlands Organization for Scientific Research (BIT), the Schure-Beijerinck-Popping Fonds, the Dobberke Stichting, and the German Ornithologists' Society (A.H.). A.H. is currently supported by a Rubicon postdoc fellowship (825.13.022) from the Netherlands Organization for Scientific Research and is associated with the Centre for Animal Movement Research (CAnMove), which is financed by a Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund University.

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Associate Editor: Robert Dudley
Editor: Judith L. Bronstein

An adult color-ringed male skylark (*Alauda arvensis*) in the Aekingerzand study population in the Netherlands. This individual was ringed as a nestling and returned to breed in subsequent years. The skylark's particularly long back toe claw makes it possible to determine the wintering strategy by analyzing stable isotopes from claw material. Photo by Rob Voesten.